EVALUATION OF DIFFERENT SORGHUM GENOTYPES FOR DROUGHT RESISTANCE

By

PHODISO L. GAOSEGELWE

B.S., Kansas State University, 1985

A MASTER'S THESIS

submitted in partial fulfillment of

the requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

Kansas State University
Manhattan, Kansas

1988

Approved by:

M. B. Kirkham

Major Professor

LD
2668
.T4
AGKN
1988
G36
c. 2

A11208 232610

TABLE OF CONTENTS

LIST OF TABLES

Page

Page

ACKNOWLEDGEMENTS

Financial support was provided by an agreement between the International Agricultural Programs at Kansas State University and the government of Botswana. The help of Dr. William J. Jorns, Assistant Director of the International Agricultural Programs, is particularly appreciated. The assistance of Dr. Paula J. Bramel-Cox, Committee Member, is also much appreciated. She suggested the study, designed the experiment, provided the seeds of the sixteen genotypes used in the study, determined measurements to be taken, loaned the LI-1600 instrument (steady-state porometer) used in the study, and guided the statistical analysis. Dr. Richard L. Vanderlip, Committee Member, is also thanked for his extensive help with the thesis. The thoughtful insights concerning the study, provided by Dr. Francis L. Barnett, Committee Member, also are gratefully recognized. I also thank Dr. Gary M. Paulsen for letting me work in his laboratory. The support of my family in Botswana is also greatly appreciated.

INTRODUCTION

Drought is one of the most prevalent environmental stresses which limits crop production on 25% of the world's land. Other stresses and areas affected are: shallow soils, 22%; mineral stress, 20%; permanent freezing, 13%; excess water, 11%; no stress, 9% (Christiansen, 1982). Genetic modification of plants to grow and yield under unfavorable conditions is one solution to problems of environmental stress.

Sorghum [Sorghum bicolor (L.) Moench] is the leading cereal grain in Africa and is also important in the United States, India, Pakistan, and China. It is grown in many other countries. It is produced mainly in hot, dry regions (Martin, 1971). The major environmental factor limiting the range of adaptation of sorghum is drought. Sorghum yields could be enhanced if genotypes could be grown in areas now too dry to support growth.

Several studies show that physiological responses of sorghum are related to drought resistance. Peacock et al. (1985) screened over 700 lines of sorghum, including advanced breeding materials, under severe drought. His technique used a physiological approach. Visually observed differences in resistant and susceptible genotypes (e.g., resistance to desiccation, ability to produce grain) were associated with physiological traits, including leaf water

potential and stomatal conductance. Jika et al. (1980) obtained correlations between yield and physiological characteristics of twelve sorghum varieties under drought. The correlations were at best low and usually non-significant. Ravindranath and Shiv Raj (1983) found that sorghum varieties with light green leaves (IS 3962, M 35-I, IS 2394) yielded more grain under drought than varieties with dark green leaves (IS 474, CS 3541), which suggested a relationship between amount of chlorophyll and drought resistance. These studies indicate that drought resistance can be based on measurable physiological responses.

Landrace sorghums might be used as a link between wild species and present-day (adapted) sorghums to improve growth under environmental stress (Blum, 1987). Adapted sorghums have three genes for maturity and three genes for height (Dr. P. Bramel-Cox, personal communication, 29 June 1988). Landraces are plants used in agriculture before the era of modern plant breeding (i.e., before the use of systematic selection and controlled breeding programs) and are well known in a locality with morphological identity, diversity, and adaptability (Jain, 1983). They are still used. Little work has been done with landraces, although there have been reports on the comparative physiology of wild progenitors and modern cultivars of crop plants, especially wheat and rice (Blum, 1987). Blum and Sullivan (1986) studied landraces of sorghum which had evolved along gradients of

rainfall in Africa. Six sorghums were from Mali and seven were from the Sudan. The landraces differed in drought resistance. Drought resistance, in terms of less growth inhibition under stress, was higher in races from dry regions than races from humid regions. Blum and Sullivan (1986) measured physiological traits, including carbon dioxide exchange rate, transpiration, stomatal resistance, leaf water potential, and osmotic adjustment. Landraces from drier regions had greater osmotic adjustment than landraces from humid regions.

The objective of this research was to determine, using physiological measurements, whether wild sorghums and landraces can be used as sources of drought resistance for breeding programs. A secondary objective was to compare wild and landrace sorghums with the sorghums already being used in the United States. Attainment of those objectives required examination of genotype-by-water-treatment interactions. This literature review will not deal comprehensively with the physiological aspects of plant resistance to environmental stress, because it has been documented extensively (Blum, 1980, 1982, 1983, 1985; Blum et al., 1978; Krieg, 1983; Quizenberry, 1982). Rather the literature review will examine only the physiological responses which were studied in this research.

LITERATURE REVIEW

Stomatal Resistance

Stomatal resistance is an important physiological trait. If plants are stressed, stomata close and the diffusion of water vapor from the stomata is reduced, thereby increasing stomatal resistance. Measurement of stomatal resistance can give an indication of plant stress, even before visible symptoms of injury occur.

Stomatal sensitivity to water deficit varies among sorghum genotypes. Henzell et al. (1975) measured stomatal resistance of 23 genotypes of sorghum in a controlled environment chamber. Stomatal sensitivity to water stress of a genotype was compared to that of a check genotype (M35-1) grown in the same pot. Stomatal resistance of the 23 genotypes varied as soil water potential decreased (became more negative). Stomata on the adaxial surface were more sensitive to reduction in soil water potential than those on the abaxial surface. Shallu was the most sensitive genotype and I.S. 1598C was the least sensitive relative to M35-1. The stomata did not reach maximum opening during a day until the lights had been on for two or three hours. This delay became greater as the soil dried out. Teare and Kanemasu (1972) found that the stomata of well watered, field-grown sorghum (Pioneer 846) did not reach maximum opening until about 10 hours after sunrise.

In a subsequent study, Henzell et al. (1976) determined stomatal resistance in four lines (Shallu and Alpha, considered sensitive, and I.S. 1598C and M35-1, considered insensitive) and their F_1 hybrids. Stomatal sensitivity varied among the parents during progressive water deficit. Stomatal conductance (reciprocal of stomatal resistance) of leaves of Alpha and Shallu decreased rapidly as leaf water potential declined, whereas it declined more slowly in I.S. 1598C and M35-1. In general, the behavior of the F_1 hybrids was similar to that of the more sensitive parent. The results suggested that stomatal sensitivity was an important element of genotypic variation in drought resistance.

Wright et al. (1983) also found genotypic differences in stomatal resistance between Dekalb E-57 (with reputed drought resistance) and TX-671 (recommended for irrigated areas). Dekalb E-57 maintained stomatal opening and turgor to a lower leaf water potential than TX-671 (-2.0 MPa for Dekalb E-57 as compared to -1.4 MPa for TX-671).

Stomatal resistance has been related to photosynthesis. If stomata are open, carbon dioxide can be taken up and photosynthesis can occur. Conversely, if stomata are closed, little carbon dioxide is taken up and photosynthesis is reduced. Krieg and Hutmacher (1986) studied the sorghum hybrid ATX623 X TX430 under a range of irrigation levels. They found photosynthetic rate changes that responded to stomatal conductance to maintain a constant intercellular

carbon dioxide concentration. Garrity et al. (1984) measured stomatal resistance and photosynthesis in three hybrids, RS 626, NB 505, and NC+ 55X, under drought stress. Stomatal resistance was sensitive to small reductions in leaf water potential during the vegetative period. During the reproductive period, the stomata became insensitive to leaf water potential and remained open at low leaf water potentials. Kanemasu et al. (1973) studied sorghum (Pioneer 846) and measured stomatal resistance, leaf water potential, and soil water deficit. All measurements correlated with drought stress. However, stomatal resistance changed more than either leaf or soil water potential. Additionally, a decline in photosynthesis occurred with a large increase in resistance. They said that only stomatal resistance on the abaxial surface of the first fully expanded leaf at midday is necessary to follow plant water deficits in sorghum. However, if one wants to estimate evapotranspiration from measurements of stomatal resistance, the more leaves that one can measure, the more accurate the estimates of evapotranspiration will be (Brun et al., 1973). In addition, one must take into account time of planting. Blum (1972) found that early-planted sorghum (four hybrids: RS-610, 6674, 6681, 6841) had a lower stomatal resistance compared to late-planted sorghum, because of date of planting.

Since stomatal resistance often is inversely related to growth (photosynthesis), it may be possible to increase growth by increasing stomatal opening (decrease stomatal resistance). Studies by Szeicz et al. (1973) indicate this. They made measurements of stomatal resistance in sorghum (RS 610) grown at College Station, Texas. Their results suggested that by doubling crop density (doubling the current practice of planting 90-cm wide rows) and irrigating to maintain stomatal resistances near minimum, sorghum yields might be increased by about 100%, probably due to increased stomatal opening.

However, if water is limited, closing stomata may conserve water. Compared to other species, sorghum is classified as a drought-resistant crop (Krieg and Hutmacher, 1982), and its resistance may be related to sorghum's ability to close stomata. For example, Teare and Kanemasu (1972) contrasted sorghum and soybean and found that sorghum was able to close its stomata more than soybean and thus conserve water, even though sorghum had a larger root system than soybean.

<u>Transpiration</u>

The period of highest water use (greatest amount of water lost by transpiration) by sorghum is during the reproductive or half-bloom stage (Kanemasu, 1977). Brun et al. (1972) showed that the proportion of water lost as

transpiration was closely related to leaf area index (LAI); transpiration was about 50% of the total evapotranspiration at an LAI of 2 and was as much as 95% at an LAI of 4. On a seasonal basis, evaporation contributes about 15 to 20% to the total evapotranspiration (Kanemasu et al., 1976). van Bavel et al. (1984) developed a model to predict transpiration from sorghum. During a 50-day growth period, the model calculated that transpiration was 3.5 mm per day for the first 38 days and for the remaining 12 days, when severe water stress had developed, it was only 1.6 mm per day.

Transpiration rate also is affected by soil moisture. Sumayao et al. (1977) observed that transpiration rates were reduced when available soil moisture was less than or equal to 35% of the maximum. Above that level, transpiration was dependent upon the amount of energy from the sun, and the rate increased at air temperatures higher than 33°C. Below the critical soil-moisture level, leaf water potential decreased and the resistance to vapor transport increased, which reduced transpiration rates. Blum and Arkin (1984) found that below 20% available soil water, transpiration was controlled mainly by a reduction in leaf area through leaf senescence.

Leaf Temperature

Leaf or canopy temperature can indicate how much water a crop is losing. If stomata are open, transpirational cooling occurs and canopy temperature should be below air temperature. Conversly, if stomata are closed, leaves are not cooled and canopy temperature should be above air temperature. Consequently, one should be able to use canopy temperature, along with stomatal resistance, to characterize the water status of a crop. To substantiate this point, Sumayao et al. (1980) found that leaf minus air temperature was a useful indicator of water stress in sorghum. They measured evapotranspiration, soil water content, stomatal resistance, leaf water potential, and air and leaf temperatures of cultivar SG-40GBR. When more than 35% of the available soil moisture had been depleted, the leaves lost turgor, stomatal resistance increased, and leaf temperatures rose above air temperatures because of reduced transpiration rates. van Bavel and Ehrler (1968) found that in a hot and dry environment (Arizona) leaves of well watered sorghum (RS-610) were consistently several degrees cooler than the ambient air, even in the middle of the day when radiant energy was high. Kirkham et al. (1985) in Kansas also found that sorghum (Prairie Valley 535 GR), grown in years with above-normal rainfall, had canopy temperaures cooler than air. Leaves ranged from 0.5 to 5.0^{o}C cooler than air. Stone et al. (1975) pointed out that

canopy temperature can change quickly if clouds are present. Temperature fluctuations of $3^{o}C$ within 3 min were observed during short-term changes in solar radiation.

Canopy temperature and height have been studied. Owonubi and Kanemasu (1982) measured canopy temperature of isolines of sorghum (White Sooner Milo) varying in height. Dry matter yields were in direct relation to the isoline heights. Dwarf plants consistently had the warmest canopy temperatures. Tall plants had the highest evapotranspiration.

Chaudhuri and Kanemasu (1982) did a field study in Kansas to determine the effects of a soil moisture gradient on four hybrids of sorghum (G-623 GBR, RS 626, RS 671, A 28+). Plant height, dry matter, and leaf area index decreased as watering level decreased. Higher stomatal resistance and lower water potential were associated with decreasing plant height and decreasing leaf area index. Canopy temperature of the water-stressed sorghum was generally 3.2^{o} to $3.7^{o}C$ warmer than canopy temperature of well watered plants. Canopy temperature also correlated well with water use by all hybrids. The average canopy minus air temperature was positive for hybrids receiving less than 25 cm water (irrigation plus precipitation) during the growing season, which corresponded to soil moisture values of 0.32 maximum available. In another study in Kansas with the same genotypes, Chaudhuri and Kanemasu

(1985) found that A 28+ had the highest stomatal resistance and seasonal canopy temperature, resulting in lower grain yield.

Chaudhuri et al. (1986) also used canopy temperature to try and select drought-resistant genotypes of sorghum during a two-year study in Yuma, Arizona. In 1983 and 1984, 219 and 27 genotypes of sorghum were studied, respectively. Warmer genotypes produced viable heads furthest from the irrigation sprinkler source. Their results suggested that plant temperatures indicate plant water use and yield. They concluded that breeders might select varieties suited for arid regions by using canopy-temperature measurements.

Injury to Cell Membranes

Under drought, it is important that cell membranes remain stable and do not break down. The rate of injury to cell membranes by drought may be estimated through measurement of electrolyte leakage from the cells (Sullivan, 1972; Sullivan and Ross, 1979). The method is based on dehydration *in vitro* of leaf discs by a solution of polyethylene glycol and a subsequent measurement of electrolyte leakage into an aqueous medium. Blum and Ebercon (1981) found that drought and heat tolerance were not correlated in wheat, but they were in sorghum. Sullivan and Ross (1979) observed that M35-1 sorghum was superior in both drought and heat tolerance tests than RS 626 sorghum.

M35-1 is a tall sorghum from India with previously reported drought and heat resistance. However, in another study with 12 sorghums, Sullivan and Ross (1979) saw no significant correlations between desiccation and heat tolerance. Majerus (1987) studied eight sorghum inbreds, 15 F_1 hybrids, and five commercial sorghum hybrids and found genotypic differences in cellular membrane strength at the flag-leaf stage of development. He also found that cellular membrane strength was correlated with the ability of leaves to stay green during drought.

Leaf Water Potential

Variations in leaf water potential among genotypes of sorghum under water stress have been found (Ackerson et al., 1980; Blum, 1974; Stout and Simpson, 1978). Averaging leaf water potential over the whole stress cycle gives a better estimate of response to drought than a single measurement obtained at peak stress, although genotypes usually maintain their relative rankings as leaf water potential decreases with increasing stress (Blum, 1982).

The pressure chamber is the standard field method for measuring leaf water potential, but it is too slow to use in screening work. Blum et al. (1978) developed a faster, indirect method as an aid in selection. They made low-altitude, aerial, infrared photographs of a stressed sorghum breeding nursery. The color saturation of

individual genotype canopies in the photographs was related to leaf water potentials.

Another way to obtain fast measurements of leaf water potential is to use the hydraulic press. It is highly portable, unlike the pressure chamber. Hicks et al. (1986) compared sorghum leaf water potential of six lines (TX599, TX7000, B35, SC325, SC630, 77CS1, R6956) measured with a pressure chamber or a hydraulic press. They used two endpoints with the hydraulic press. The first endpoint was when water exuded from one vein and the second endpoint was when water exuded from all veins on both sides of the leaf. The results showed that the hydraulic press and the pressure chamber measurements agreed well in the range of -0.5 to -3.5 MPa of leaf water potentials, when the second endpoint was selected for the hydraulic press.

Myers et al. (1984) measured water potential, stomatal conductance, and extension rates of leaves of four sorghums (Quicksilver, Texas 610SR, E57, Q7844) under different irrigation regimes. Pre-dawn leaf water potential, noon leaf water potential, noon stomatal conductance, and daily leaf extension rates, between floral initiation and physiological maturity, diverged gradually in response to irrigation regimes. Noon leaf water potential and stomatal conductance fluctuated from day to day, perhaps in response to variation in saturation deficit. Richardson and McCree (1985) compared sorghum plants (BTX616) exposed to both salt

and water stress. Salinized sorghum plants were able to maintain leaf expansion down to lower water potentials than drought stressed plants. Leaf area expansion became zero at a water potential of -2.1 MPa in salinized plants compared with -1.2 MPa in the nonsalinized plants.

Several physiological changes that occur under water stress have been related to sorghum leaf water potentials. Teare et al. (1974) found that nitrate reductase activity, a sensitive indicator of water stress, was reduced in sorghum (Pioneer 846) under water stress. Leaf water potentials were also reduced. Durley et al. (1983) measured concentration of abscisic acid (ABA) in leaves of nine sorghum genotypes grown in the field under drought. The nine genotypes were: NK300, IS1037, CSH1, CSH6, CSH8, M35-1, V302, CSV5, CS3541. NK300, CSH1, CSH6, and CSH8 are hybrids. NK300, IS1037, CSH1, and CSH6 are early-maturing types. They found that M35-1 has some drought resistance and said that CSV5, V302, and CS3541 are believed to be susceptible to drought. They found that, although hormone concentrations were similar in irrigated plants, there was genotypic variation in drought-stressed plants. ABA concentrations in leaves of drought-stressed plants were related to grain yield. Also the slopes of regression lines of ABA on leaf water potential in stressed genotypes were related to yield. They suggested that it might be possible to evaluate drought resistance of different sorghum

genotypes by examination of ABA concentrations in leaves. However, Huda et al. (1987) compared CSH8 and M 35-1 and found that grain yields of CSH8 were higher than those of M 35-1 under both irrigated and drought-stressed conditions, in contrast to the results of Durley et al. (1983), who found that M35-1 had drought resistance.

MATERIALS AND METHODS

Sixteen genotypes of sorghum belonging to one of three groups (wild, landraces, adapted), were used in the study (Harlan and de Wet, 1972). Six were wild, four were

Table 1. Genotypes of sorghum used in the study.

Wild sorghums [S. bicolor ssp. arundinaceum]

12-26 race virgatum (from Egypt)

IS14250 race verticilliflorum (from Angola)

IS14635 race verticilliflorum (from Ethiopia)

IS14359 race arundinaceum (from Malawi)

IS14485 race aethiopicum (from the Sudan)

IS14329 race arundinaceum (from South Africa)

Landraces sorghums [S. bicolor ssp. bicolor]

Segaolane (from Botswana)

PI494534

PI494544

PI494551

Adapted sorghums [S. bicolor ssp. bicolor]

Non-elite

SC 35-6

SC 118

Elite

Drought sensitive

Redlan

IA 25

Drought tolerant

KS 65

IA 28

---

landraces, and six were adapted (Table 1). Wild sorghums often have little potential for conventional gene transfer to cultivated sorghums, but may carry genes for resistance to drought (Jain, 1983). Landrace sorghums, as stated before, are sorghums used in agriculture before the time of modern plant breeding and are known in a locality (Jain, 1983). One of the landraces used in the study, Segaolane, from Botswana, has been particularly well studied (Rees, 1986a, 1986b; Jones, 1987a, 1987b). Segaolane is the name of the most common landrace line. Because of this, many farmers in Botswana say that their sorghum is Segaolane (John M. Peacock, personal communication, 12 November 1987). There were two types of adapted sorghums: non-elite and elite. Non-elite, adapted sorghums are adapted to this region based upon maturity and height, but are unimproved for grain yield or other traits. Elite, adapted sorghums are publically released parent lines. The four elite, adapted sorghums used in the study were classified as either drought sensitive (Redlan, IA 25) or drought tolerant (KS 65, IA 28).

Two experiments were done, both in the same greenhouse located at Kansas State University, Manhattan, Kansas.

Results from the first experiment (11 July - 15 Nov. 1986) will not be presented because only one physiological trait (stomatal resistance) was measured and the harvest samples were accidentally thrown away by a technician. Thus, the only growth measurement obtained in the first experiment was height. In the second experiment (9 May - 15 Aug. 1987), day temperature varied from 25 to 35^{o}C and night temperature varied from 16 to 24^{o}C. Relative humidity varied from 25 to 99%. Seeds were planted on 9 May 1987 and started to emerge on 15 May 1987. On 20 May 1987, seeds of genotypes that did not emerge were replanted. No adjustments were made for differences due to planting dates. Seeds were planted in a commercial greenhouse mixture (Sunshine Mix, Swecker-Knipp, Inc., Topeka, Kansas). The N, P, K, and pH of the mixture, as determined by the Plant and Soil Testing Laboratory, Kansas State University, which used standard methods of analyses, are shown in Table 2.

Table 2. Analysis of the commercial greenhouse mixture used in the study.

	Mix used in 1987 expt.
NO_3-N, µg/g	42
P (available), µg/g	>100
K (exchangeable), µg/g	300
pH	5.5

The soil was placed in large, plastic pots (6000 cm^3 or 21 cm in diameter; 21 cm in height). Plants were thinned to one plant per pot on 30 May 1987.

The soil was kept well-watered from planting (9 May 1987) until 11 June 1987. After 11 June 1987, two watering regimes were maintained. Half of the pots were kept well watered and the other half were not well watered (the "drought-stressed" plants). The well watered plants were watered every 4 to 8 days and drought-stressed plants were watered every 11 to 14 days (Table 3). The drought-stressed plants were watered to keep them from wilting severely.

Table 3. Dates of measurements and watering of the sorghum in the 1987 study.

Date	
9 May	Seeds planted
15 May	First emergence
20 May	Seeds of genotypes that did not emerge replanted
11 June	All pots watered
16 June	Well-watered pots watered
18 June	Height measured
23 June	Height measured; all pots watered
28 June	LT^+, DR^+, CD^+, TR^+, $LW\psi^+$, and injury to cell membrane measured
30 June	Well-watered pots watered; following genotypes flowering: Segalone, SC118, Redlan, KS65, 12-26
1 July	$LW\psi$ measured
6 July	All pots watered; following genotypes flowering: IS14359, IA25
8 July	DR, CD, TR, LT, $LW\psi$ measured
9 July	Height measured
10 July	Well-watered pots watered
15 July	All physiological traits measured, well-watered pots watered
17 July	DR, CD, TR, LT measured
20 July	DR, CD, TR, LT measured
22 July	DR, CD, TR, LT measured
23 July	DR, CD, TR, LT, $LW\psi$ measured; all pots watered
24 July	DR, CD, TR, LT measured

25 July	DR, CD, TR, LT, height measured
27 July	DR, CD, TR, LT, LWψ measured; well-watered pots watered
4 August	Well-watered pots watered
7 August	DR, CD, TR, LT measured
13 August	Injury to cell membrane measured
15 August	Harvest

+LWψ = leaf water potential; DR = diffusive resistance; CD = stomatal conductance, TR = transpiration; LT = leaf temperature.

Differential watering regimes continued until 15 Aug. 1987. They were stopped when all physiological measurements were completed. Physiological measurements were taken on a recently matured leaf, usually the second-from-the top, until the last leaf was fully emerged, when measurements were taken on it. Leaves were always green when measurements were taken. Measurements were not taken on leaves that were senesced. Stomatal resistance was determined with a steady state porometer (LI-1600, LI-Cor, Inc., Lincoln, Nebraska), which also gave concurrent measurements of transpiration and leaf temperature. These three measurements were made on eleven days ranging from 44 to 84 days after the first plants began to emerge. The dates of measurement were 28 June; 8, 15, 17, 20, 22, 23, 24, 25, 27 July; and 7 Aug. 1987. Measurements of stomatal resistance were made on the abaxial (lower) leaf surface,

because stomatal density is higher on the abaxial leaf surface than on the adaxial leaf surface (Liang et al., 1975).

Percent injury to cell membranes was determined three times (28 June, 15 July, 13 Aug. 1987) by the technique of Sullivan (Sullivan, 1972; Sullivan and Ross, 1979), as modified by Majerus (1987). Leaf water potential was estimated by using a hydraulic press (Model J-14 Press, Campbell Scientific, Inc., Logan, Utah). The second endpoint was used (when water exudes from all veins on both sides of the leaf). Measurements of leaf water potential were made on 28 June, and 1, 8, 15, 23, 27 July 1987.

Height was measured, from the soil surface to the tip of the last emerged leaf (extended) or to the tip of the head, on 8, 18, 23 June; 9 and 25 July 1987, and plants were harvested on 15 Aug. 1987. Plants were dried to constant weight at 80°C for three days in ovens at the Agronomy Farm, Kansas State University, Manhattan. Total dry weight and grain weight were determined.

The design was a randomized block with a split-plot arrangement. Whole plots were the two water treatments, drought-stressed and well-watered. The subplots and repeated measures on the same plot consisted of the entries and sample dates, respectively. Whole plots and subplot treatments were randomly assigned separately. Experimental units were pots. Whole plots were watering regimes and the

genotypes were the subplot. The 1987 experiment had three replications (blocks), two watering regimes, and 16 genotypes on 96 plots. The overall experimental model for each year was:

$$Y_{ijkl} = \mu + B_i + W_j + G_k + D_l + WG_{jk} + WD_{jl} + GD_{kl} +$$

$$WGD_{jkl} + e_{ijkl} .$$

Y_{ijkl} represents each individual observation in the l^{th} date, k^{th} genotype, j^{th} watering regime, and i^{th} block. The symbols: μ, B, W, G, D, WG, WD, GD, WGD, and e represent the overall population mean, the effect due to: block, water, genotype, date, water x genotype, water x date, genotype x date, water x genotype x date, and experimental error, respectively. Data were analyzed using an analysis of variance (SAS Institute, Inc., SAS Circle, P. O. Box 8000, Cary, North Carolina 27511-8000). The experimental error terms used for the water effect was error A.

Genotype and water x genotype effects were tested using error B. Sample date, water x date, genotype x date, and water x genotype x date were tested with error C. Separate analysis of variance of each sample date was conducted for those traits (leaf water potential, leaf temperature, stomatal resistance, and stomatal conductance) that had significant entry (genotype) and/or entry interaction(s)

differences in the combined analysis for the trait. Individual dates with non-significant genotypic effects were not included in the combined analysis of the trait. Homogeneity of error variances was tested. All error variances were homogeneous and, therefore, the combined analysis for the different traits was performed. Analysis of variance for leaf water potential was calculated on natural-log transformed data to achieve independent means and homogeneous variances.

RESULTS AND DISCUSSION

Since the objective of the study was to determine whether the wild and the landrace sorghums can be used as sources of drought resistance, only those traits (physiological and growth) with significant genotype, genotype x water, genotype x date, and genotype x water x date interactions will be discussed. Significant differences due to water treatment without significant genotype and/or genotype interaction(s) reveal that there was significant difference between the watering regimes for the measured traits. The same is true for significant differences due to sample dates because there was a significant difference among the sampling dates for the measured traits. Data for injury to cell membranes (1987) and transpiration (1987) will not be discussed because only the sample dates were significantly different. The results and discussion are presented in two sections. The first section discusses the physiological traits and the second section deals with the growth traits.

Physiological Traits:

Five sample dates, out of six (all dates except 27 July; see Table 3), were used to compile Table 4 (analysis of variance table for leaf water potential), eight sample dates, out of eleven (all dates except 28 June, 23 & 27 July;

see Table 3), were used for Table 5 (analysis of variance table for leaf temperature), and one sample date (8 July) for stomatal resistance and stomatal conductance, out of eleven dates, was used for Table 6 (analysis of variance table for stomatal resistance and stomatal conductance). Genotypic differences were significant for the four traits (Tables 4 to 6). Significant genotypic group response shows that the genotypes within the group (wild, landraces, non-elite, drought-sensitive or drought-resistant elite) did not respond similarly for the measured trait, while non-significance within the group indicates homogeneity within the group. Significant differences among groups represented the different responses among the groups for the measured trait. Significant differences among the genotypes were due to the differences within the wild group and within the landrace group for leaf water potential; within the wild group, and among the groups for leaf temperature; within the wild group, within the landrace group, and among the groups for stomatal resistance; and within the wild group, and among groups for stomatal conductance (Tables 4 to 6).

Significant interaction within the genotypes indicates that they do not respond similarly in different water treatments, sample dates (growth stages), or both, and, therefore, these should be considered when evaluating sorghum for drought resistance. Genotype x water

Table 4. Combined analysis of variance mean squares for leaf water potential from the sixteen entries in five sample dates in well-watered and drought-stressed treatments in 1987.

Source	df	MS
Water (Wat)	1	1.86
Blk (Block)	2	0.12
Error (A)	2	0.28
Genotype (Gen)	15	0.40**
Within Wild	(5)	0.75**
Within landraces	(3)	0.42**
Within non-Elite	(1)	0.29
Within DS Elite+	(1)	0.23
With DR Elite×	(1)	0.12
Among Groups	(4)	0.09
Wat & Gen	15	0.05
Within Wild x Water	(5)	0.10
Within Landraces x Water	(3)	0.06
Within non Elite x Water	(1)	0.01
Within DS Elite+ x Water	(1)	0.01
Within DR Elite× x Water	(1)	0.01
Among Groups x Water	(4)	0.01
Error (B)	60	0.09
Date	4	10.44**
Water x Date	4	0.98**
Gen x Date	60	0.06**
Within Wild x Date	(20)	0.05
Within Landraces x Date	(12)	0.04
Within non Elite x Date	(4)	0.03
Within DS Elite+ x Date	(4)	0.04
Within DR Elite× x Date	(4)	0.04
Among Groups x Date	(16)	0.10**
Wat x Gen x Date	60	0.04
Within Wild x Water x Date	(20)	0.05
Within Landraces x Water x Date	(12)	0.03
non Elite x Water x Date	(4)	0.05
DS Elite+ x Water x Date	(4)	0.03
DR Elite× x Water x Date	(4)	0.04
Among Groups x Water	(16)	0.02
Error (C)	256	0.03
C.V.(%)(Error C)		3.45

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
+ Within Drought-Sensitive Elite
× With Drought-Tolerant Elite
§ Analysis of variance calculated on natural log transformed data.

Table 5. Combined analysis of variance mean squares for leaf temperature from the sixteen entries in eight sample dates in well-watered and drought-stressed treatments in 1987.

Source	df	MS
Water (Wat)	1	10.3
Blk (Block)	2	30.2
Error (A)	2	4.4
Genotype (Gen)	15	12.8**
Within Wild	(5)	21.6**
Within landraces	(3)	5.1
Within non-Elite	(1)	1.3
Within DS Elite+	(1)	0.9
With DR Elite×	(1)	0.4
Among Groups	(4)	16.5**
Wat & Gen	15	2.2
Within Wild x Water	(5)	3.6
Within Landraces x Water	(3)	0.9
Within non Elite x Water	(1)	0.5
Within DS Elite+ x Water	(1)	0.03
Within DR Elite× x Water	(1)	1.5
Among Groups x Water	(4)	2.6
Error (B)	60	1.8
Date	7	72.1**
Water x Date	7	5.7**
Gen x Date	105	1.6
Within Wild x Date	(35)	3.9**
Within Landraces x Date	(21)	0.3
Within non Elite x Date	(7)	0.2
Within DS Elite+ x Date	(7)	0.3
Within DR Elite× x Date	(7)	0.3
Among Groups x Date	(28)	0.78
Wat x Gen x Date	105	1.3
Within Wild x Water x Date	(35)	3.1**
Within Landraces x Water x Date	(21)	0.2
non Elite x Water x Date	(7)	0.1
DS Elite+x Water x Date	(7)	0.1
DR Elite× x Water x Date	(7)	0.1
Among Groups x Water x Date	(28)	0.7
Error (C)	448	1.6
C.V.(%)(Error C)		4.5

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

+ Within Drought-Sensitive Elite

× With Drought-Tolerant Elite

Table 6. Combined analysis of variance mean square for stomatal resistance (DR) and stomatal conductance (CD) from the sixteen entries in one sample date in well-watered and drought-stressed treatments in 1987.

Source	df	Resis-tance	Conduc-tance
Water (Wat)	1	4.49	0.001
Blk (Block)	2	24.25	0.03
Error (A)	2	3.40	0.01
Genotype (Gen)	15	6.30**	0.01**
Within Wild	(5)	7.59**	0.01**
Within landraces	(3)	4.92*	0.004
Within non-Elite	(1)	0.10	0.0003
Within DS Elite+	(1)	4.37	0.003
With DR Elite×	(1)	0.51	0.001
Among Groups	(4)	9.20**	0.01**
Gen & Wat	15	2.49	0.002
Within Wild x Water	(5)	0.77	0.002
Within Landraces x Water	(3)	0.69	0.001
Within non-Elite x Water	(1)	0.01	0.0000
Within DS Elite+ x Water	(1)	0.02	0.00001
Within DR Elite× x Water	(1)	1.1	0.0003
Among Groups x Water	(4)	7.56**	0.004
Error (B)	60	1.55	0.002
C.V.(%)(Error B)		20.77	25.17

* Significant at the 0.05 probability level
** Significant at the 0.01 probability level
+ Within Drought-Sensitive Elite
× With Drought-Tolerant Elite

interaction for the four traits (leaf water potential, leaf temperature, stomatal resistance, and stomatal conductance) was not significant. Significant sample date differences were found for all the physiological traits. Sample date x water interactions were significantly different for leaf water potential and leaf temperature (Tables 4 and 5). The significant differences among the genotypes were due to the differences within the wild group and among the groups for leaf temperature (Table 5). The significant differences among the genotypes were due to the differences within the wild group, within the landrace group, and among the groups for stomatal resistance (Table 6). Significant differences among the genotypes were due to the differences within the wild group and among groups for stomatal conductance (Table 6).

Table 7 shows the mean leaf water potential for the five groups of sorghum on the different dates of measurement. Means were different on each date. No one group consistently had a high or a low leaf water potential. Table 8 shows mean leaf water potential for the well-watered and drought-stressed plants on the different dates of measurement. Means were different on 8 July, 15 July, and 23 July. Potentials were low for the drought-stressed plants on 23 July because the measurements were taken just before watering on 23 July. Potentials varied within water

Table 7. Means of leaf water potential for the five groups of sorghum on sample dates in 1987. Well-watered and drought-stressed treatments have been averaged together.

Group	28 June	1 July	8 July	15 July	23 July
			MPa		
Wild	-0.83	-1.22	-1.70	-1.69	-2.35
Landraces	-0.89	-1.43	-1.84	-1.71	-2.04
Non-elite	-0.89	-1.42	-1.86	-1.78	-1.83
Drought-sensitive elite	-0.89	-1.52	-1.78	-1.75	-2.14
Drought-resistant elite	-0.91	-1.49	-1.79	-1.58	-1.95

LSD for two groups within the same date or between two different dates = 0.01.

Table 8. Means of leaf water potential for sorghum under well-watered and drought-stressed conditions on sample dates in 1987. The five groups of sorghum have been averaged together

Water regime	28 June	1 July	8 July	15 July	23 July
	MPa				
Well-watered	-0.88	-1.42	-1.47	-1.76	-1.69
Drought-stressed	-0.88	-1.41	-2.11	-1.64	-2.49

Two dates in the same water treatment (LSD = 0.01)

Two water treatements within the same date or between two different dates (LSD = 0.01)

treatment according to time of watering. The potentials tended to fall each day past watering and then rose after watering. The potentials ranged from -0.88 to -2.49 MPa, with the higher potentials occurring early in the growth cycle and the lower potentials occurring late in the growth cycle.

The significant differences among the genotypes were due to the differences within the wild group and within the landrace group for leaf water potential (Table 4). Table 9 shows the mean leaf water potential of the wild sorghums and landrace sorghums. Within the wild sorghums, IS14329 (from South Africa) had the lowest water potential and 12-26 (from Egypt) had the highest water potential. Within the landraces, PI494544 (SN 537) had the lowest potential and Segaolane (from Botswana) had the highest potential. The drought-resistant elite sorghums did not have a consistently higher or lower potential than did the drought-sensitive elite sorghums (Table 7).

Table 10 shows the mean leaf temperature of the wild sorghums under well-watered and water-stressed conditions on different dates of measurement. On each measurement day, the drought-stressed plants had a lower leaf temperature then did the well-watered plants, except for 8 and 22 July (note horizontal line labeled "Mean" in Table 10). On these two dates, differences were small ($0.3^{o}C$). On 7 Aug., the

Table 9. Means of leaf water potential for wild sorghums and for the landrace sorghums. Well-watered and drought-stressed treatments have been averaged together over time.

Genotype	Leaf water potential
	MPa
<u>Wild sorghums</u>	
12-26	-1.18^{f+}
IS14250 (40-114)	-1.57^{c}
IS14635 (74-150)	-1.39^{e}
IS14359 (83-170)	-1.75^{b}
IS14485 (88-181)	-1.54^{d}
IS14329 (82-169)	-1.76^{a}
<u>Landraces</u>	
Segaolane	-1.35^{d}
PI494534 (SN 526)	-1.65^{b}
PI494544 (SN 537)	-1.75^{a}
PI494551 (SN 543)	-1.43^{c}

$^{+}$Means within a group followed by the same letter are not significantly different at the 0.05 level according to Duncan's new multiple range test.

Table 10. Means of leaf temperature of the wild sorghums under well-watered and drought-stressed conditions on sample dates in 1987.

Genotype	8 July	15 July	17 July	20 July	22 July	24 July	25 July	7 Aug.	Mean
	°C								
	Well-watered								
12-26	28.1	28.0	27.5	28.9	28.9	27.9	28.0	28.6	28.4
IS14250	29.3	28.6	28.4	29.8	29.8	28.4	28.6	31.1	29.2
IS14635	28.2	28.5	28.1	30.0	29.7	28.2	28.5	30.1	29.0
IS14359	29.6	29.7	28.1	29.7	30.3	28.2	29.7	31.7	29.6
IS24485	29.2	28.4	27.8	29.4	30.3	28.1	28.4	30.2	29.0
IS14329	29.5	28.2	28.5	29.5	29.8	28.5	28.2	31.1	29.2
Mean	29.0	28.6	28.1	29.6	29.8	28.2	28.6	30.5	29.1
	Drought-stressed								
12-26	28.1	26.5	27.2	28.4	29.6	28.0	26.5	29.4	28.0
IS14250	30.9	27.9	28.1	29.9	31.4	27.9	27.9	31.4	29.4
IS14635	28.6	27.5	27.5	29.1	29.8	27.7	27.5	29.8	28.5
IS14359	29.7	28.1	28.0	29.5	30.0	28.1	28.1	31.0	29.0
IS14485	28.7	27.6	27.2	28.8	29.4	28.0	27.6	29.7	28.4
IS14329	29.8	27.8	28.5	29.6	30.2	28.0	27.8	31.5	29.1
Mean	29.3	27.6	27.8	29.2	30.1	28.0	27.6	30.5	28.7

(i) LSD = 0.6 (for two dates for the same genotype withing the same water treatment.)

(ii) LSD = 4.3 (for two water treatments for the same genotype within the same date).

(iii) LSD = 3.3 (for two genotypes for the same water treatment within the same date).

mean leaf temperature of the well-watered wild sorghums was the same as the mean leaf temperature of the drought-stressed wild sorghums (30.5^oC). Under well-watered conditions, 12-26 (from Egypt) had the coolest leaf temperature (28.4^oC) and IS14359 (from Malawi) had the warmest leaf temperature (29.6^oC). Under drought-stressed conditions, 12-26 had the coolest leaf temperature (28.0^oC) and IS14250 (from Angola) had the warmest leaf temperautre (29.4^oC). Table 11 shows the means of the leaf temperature for the five groups of sorghum. Temperatures ranged from 28.1^oC to 29.0^oC, with the wild sorghums having the warmest leaf temperature and the non-elite and elite sorghums having the coolest leaf temperature. Table 12 shows the means of stomatal resistance for the five groups of sorghum under well-watered and drought-stressed conditions. Under well-watered conditions, the drought-resistant elite sorghums had the highest stomatal resistance (7.99 sec/cm) and the landraces had the lowest stomatal resistance (5.40 sec/cm). Under drought-stressed conditions, the landraces had the highest stomatal resistance (6.49 sec/cm) and the wild sorghums had the lowest stomatal resistance (5.21 sec/cm). If one compares well-watered and drought-stressed plants, the landraces had the highest stomatal resistance under drought-stressed conditions, and the other groups had a lower stomatal resistance under drought-stressed conditions compared to well-watered

Table 11. Means of the leaf temperature of the five groups of sorghum. Well-watered and drought-stressed treatments have been averaged together over time.

Group	Temperature
	°C
Wild	29.0
Landraces	28.6
Non-elite	28.1
Drought-sensitive elite	28.1
Drought-resistant elite	28.2

LSD = 0.2 (for wild vs landraces)

$$\left[0.2 = 2\sqrt{1.79\left[\frac{1}{6 \times 2 \times 3 \times 9}\right]\left[\frac{1}{4 \times 2 \times 3 \times 9}\right]}\right]$$

LSD = 0.3 (for wild vs non-elite, drought-sensitive elite or drought-resistant elite)

LSD = 0.3 (for landraces vs non-elite, drought-sensitive or drought-resistant elite)

LSD = 0.4 (for non-elite vs drought-sensitive or drought-resistant elite)

Table 12. Means of stomatal resistance of the five groups of sorghum under well-watered and drought-stressed conditions on 8 July 1987 (54 days after emergence).

Group	Stomatal resistance	
	sec/cm	
	Well-watered	Drought-stressed
Wild	5.42	5.21
Landraces	5.40	6.49
Non-elite	7.66	6.04
Drought-sensitive elite	7.04	5.49
Drought-resistant elite	7.99	5.70

LSD's for two group means at the same level of water.

(a) Wild vs landraces = 0.93

(b) Wild vs non-elite, drought-sensitive or drought-resistant elite = 1.17

(c) Landraces vs non-elite, drought-sensitive or drought-resistant elite = 1.25

(d) Non-elite vs drought-sensitive or drought-resistant elite = 1.44

conditions. Plants were watered on 6 July and measurements were taken on 8 July. Drought-stressed plants did not have a consistently higher stomatal resistance compared to well-watered plants, perhaps because the drought-stressed plants were not severely stressed on the day of measurement. Table 13 shows the means of the stomatal resistance for the landraces of sorghum. Segaolane (from Botswana) had the highest stomatal resistance (6.96 sec/cm) and PI494544 (SN 537) had the lowest stomatal resistance (4.81 sec/cm). Table 14 shows the means of the stomatal resistance for the wild sorghums. IS14250 (from Angola) and IS14329 (from South Africa) had the lowest stomatal resistances (4.35 sec/cm) and 12-26 (from Egypt) had the highest stomatal resistance (7.10 sec/cm).

Table 15 shows the means of the stomatal conductance for the five groups of sorghum. The non-elite and drought-resistant elite sorghums had the lowest stomatal conductance (0.15 cm/sec) and the wild sorghums had the highest stomatal conductance (0.21 cm/sec). Table 16 shows the means of the stomatal conductance for the wild sorghums. 12-26 (from Egypt) had the lowest stomatal conductance (0.16 cm/sec) and IS14250 (from Angola) had the highest stomatal conductance (0.27 cm/sec).

Table 13. Means of stomatal resistance for the landraces of sorghum on 8 July 1987. Well-watered and drought-stressed treatments have been averaged together.

Genotype	Stomatal resistance
	sec/cm
Segalone	6.96[a]
PI 494534	5.74[+ab]
PI 494544	4.81[b]
PI 494551	6.27[a]

[+]Means followed by the same letter are not significantly different at the 0.05 level according to Duncan's new multiple range test.

Table 14. Means of stomatal resistance for the wild sorghums on 8 July 1987. Well-watered and drought-stressed treatments have been averaged together.

Genotype	Stomatal resistance
	cm/sec
12-26	7.10[+a]
IS14250 (40-114)	4.35[c]
IS14635 (74-150)	6.27[ab]
IS14359 (83-170)	4.75[c]
IS14485 (88-181)	5.10[bc]
IS14329 (82-169)	4.35[c]

[+]Means followed by the same letter are not significantly different at the 0.05 level according to Duncan's new multiple range test.

Table 15. Means of the stomatal conductance of the five groups of sorghum. Well-watered and drought-stressed treatments have been averaged together.

Group	Stomatal Conductance
	cm/sec
Wild	0.21
Landraces	0.18
Non-elite	0.15
Drought-sensitive elite	0.16
Drought-resistant elite	0.15

Wild vs landraces (LSD = 0.02)

Wild vs non-elite, drought-sensitive elite or drought resistant elite (LSD = 0.03)

Landraces vs non-elite, drought-sensitive or drought-resistant elite (LSD = 0.03)

Non-elite vs drought-sensitive or drought resistant (LSD = 0.04)

Table 16. Means of stomatal conductance for the wild sorghums on 8 July 1987. Well-watered and drought-stressed treatments have been averaged together.

Genotype	Stomatal conductance
	cm/sec
12-26	0.16[+c]
IS14250 (40-114)	0.27[a]
IS14635 (74-150)	0.17[c]
IS14359 (83-170)	0.23[ab]
IS14485 (88-181)	0.20[bc]
IS14329 (82-169)	0.24[ab]

[+] Means followed by the same letter are not significantly different at the 0.05 level according to Duncan's new multiple range test.

Growth Traits:

The growth traits determined in 1987 were total dry weight, yield, and height. Significant water treatment differences were found for total dry weight (Table 17). Yield and height were not significantly altered by drought stress (Tables 18 and 19).

Genotypic differences were significant for all growth traits (Tables 17 to 19). Significant differences among the genotypes were due to the differences within the wild sorghums, the landraces, the non-elite sorghums, and among the groups for total dry weight. Significant differences among the genotypes were due to the differences within the landraces, the drought-sensitive elite, the drought-resistant elite, and among the groups for yield. IS14485 and IS14635, the wild sorghums from the Sudan and Ethiopia, respectively, did not yield grain under any treatment, perhaps because photoperiodic requirements were not met. Significant genotypic differences for heights were due to genetic traits (Table 19). Table 20 shows the means of the dry weight of the wild sorghums grown under well-watered and drought-stressed conditions. 12-26 (from Egypt) had the lowest dry weight under well-watered conditions. IS14485 (from the Sudan) had the highest dry weight under well-watered conditions and IS14635 (from Ethiopia) had the highest dry weight under drought-stressed conditions. Table 21 shows the means of the dry weight of

Table 17. Analysis of variance mean squares for total dry weight (DM) from the sixteen genotypes in well-watered and drought-stressed treatments in 1987.

Source	d.f.	Dry Weight
Water	1	2712.00**
Block	2	297.90
Error (A)	2	13.61
Genotype	15	903.50**
Within Wild	(5)	979.18**
Within Landraces	(3)	1274.10**
Within Non-Elite	(1)	1548.10**
Within DS Elite	(1)	3.52
Within DR Elite	(1)	37.74
Among Groups	(4)	8110.30**
Wat x Gen	15	324.80**
Within Wild x Water	(5)	310.90*
Within Landraces x Water	(3)	684.50**
Within non-Elite x Water	(1)	73.57
Within DS Elite x Water	(1)	14.30
Within DR Elite x Water	(1)	11.03
Among Groups x Water	(4)	291.20
Error (B)	60	128.50
CV (%)(Error B)		31.19

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table 18. Analysis of variance mean squares for the yield from the sixteen genotypes in well-watered and drought-stressed treatments in 1987.

Source	d.f.	MS
Water	1	30.2
Block	2	28.5
Error (A)	2	6.6
Genotype	13	140**
Within Wild	(3)	0.10
Within Landraces	(3)	40**
Within Non-Elite	(1)	25.7
Within DS Elite	(1)	37.4*
Within DR Elite	(1)	75.2**
Among Groups	(4)	391**
Wat x Gen	13	19.1**
Within Wild x Water	(3)	0.09
Within Landraces x Water	(3)	15
Within non-Elite x Water	(1)	14.6
Within DS Elite x Water	(1)	0.79
Within DR Elite x Water	(1)	17.7
Among Groups	(4)	42.5**
Error (B)	52	9.5
CV (%)(Error B)		49

*,**Significant at the 0.05 and 0.01 probability levels, respectively.

Table 19. Analysis of variance mean squares for heights (1987) from the sixteen genotypes in well-watered and drought-stressed treatments.

Sources	d.f.	MS
Water	1	8012
Block	2	53
Block x Water	2	2145
Genotype	15	12294**
Water x Genotype	15	1646
Error	60	948
CV(%)		23.71

*,** Significant at 0.05 and 0.01 probability levels, respectively.

Table 20. Means of dry weight of the wild sorghums grown under well-watered and drought-stressed conditions.

Genotype	Dry Weight	
	g/plant	
	Well-watered	Drought-stressed
12-26	9.3	15.2
IS14250 (40-114)	32.5	33.0
IS14635 (74-150)	31.7	37.6
IS14359 (83-170)	51.9	35.7
IS14485 (88-181)	58.5	30.1
IS14329 (82-169)	55.4	37.4

Genotype means at the same level of water (LSD = 18.5)

Water treatments for the same or different genotypes (LSD = 34.4).

the landraces grown under well-watered and drought-stressed conditions. Dry weight of Segaolane was not reduced by drought. Under well-watered conditions, Segaolane had the lowest dry weight and SN 526 (PI494534) had the highest dry weight. Under drought-stressed conditions, Segaolone again had the lowest dry weight, but SN 537 (PI494549) had the highest. Of the non-elite sorghums, SC 35-6 had a higher dry weight (44.1 g/plant) than SC 118 (21.4 g/plant). Table 22 shows the means of the dry weight of the five groups of sorghum. The landraces had the highest dry weight and the drought-sensitive elite sorghums had the lowest dry weight.

Table 23 shows the yield means for the five groups of sorghum under well-watered and drought-stressed conditions. The yield of the elite sorghums was reduced by drought. Under both well-watered and drought-stressed conditions, the wild sorghums yielded the least and non-elite sorghums yielded next to least. Under well-watered conditions, the drought-resistant elite sorghums yielded the most, and under drought-stressed conditions, the landraces yielded the most. Tables 24, 25, and 26 show the means of the yield of the drought-resistant elite sorghums, and drought-stressed elite sorghums, and landraces, respectively. IA28 yielded more than KS 65 (Table 24). Drought-sensitive sorghums had similar yields (Table 25). Segaolane yielded the least of the landraces (Table 26).

Table 21. Means of dry weight of the landraces of sorghum grown under well-watered and drought-stressed conditions.

Genotype	Dry weight	
	g/plant	
	Well-watered	Drought-stressed
Segaolone	21.4	26.6
PI 494534	79.5	32.8
PI 494544	63.0	43.9
PI 494551	51.3	36.7

(a) Genotype means at the same water level (LSD = 18.5)

(b) Water treatment means for the same or different genotype (LSD = 34.4).

Table 22. Means of the dry weight of the five groups of sorghum. Well-watered and drought-stressed treatments have been averaged together.

Group	Dry weight
	g/plant
Wild	35.7
Landraces	44.1
Non-elite	32.7
Drought-sensitive elite	28.9
Drought-resistant elite	33.2

Wild vs landraces (LSD = 6.0)

Wild vs non-elite, drought sensitive or drought-resistant (LSD = 7.6)

Landraces vs non-elite, drought-sensitive or drought-resistant (LSD = 8.0)

Non-elite vs drought-sensitive or drought-resistant (LSD = 9.2).

Table 23. Means of the yield of the five groups of sorghum under well-watered and drought-stressed treatments.

Group	Grain Yield	
	g/plant	
	Well-watered	Drought-stressed
Wild+	0.21	0.34
Landraces	9.0	10.1
Non-elite	3.7	3.9
Drought-sensitive elite	12.4	7.7
Drought-resistant elite	13.6	7.1

+Yield of the two wild genotypes that did not yield any grain [IS14635 (74-150) and IS14485 (88-181)] have not been included in the analysis.

LSD's for two group means at the same level of water treatments:
(a) Wild vs landraces (LSD = 1.5)
(b) Wild or landraces vs non-elite, drought-sensitive or drought-resistant (LSD = 1.8)
(c) Non-elite vs drought-sensitive or drought-resistant elite (LSD = 2.0).
(d) Two water treatment means at the same level or at different levels of genotype:
    (i) Wild vs landraces (LSD = 4.2).
    (ii) Wild or landraces vs non-elite, drought-sensitive or drought-resistant (LSD = 4.2).
    (iii) Non-elite vs drought-sensitive or drought-resistant (LSD = 6.6).

Table 24. Means of the yield of the drought-resistant sorghums. Well-watered and drought-stressed treatments have been averaged together.

Genotype	Yield
	g/plant
IA 28	12.8^{+a}
KS 65	7.8^{b}

$^{+}$Means followed by the same letter are not significantly different at the 0.05 level according to Duncan's new multiple range test.

Table 25. Means of the yield of the drought-sensitive, elite sorghums. Well-watered and drought-stressed treatments have been averaged together.

Genotype	Yield
	g/plant
IA 25	8.3[+a]
Redlan	11.8[a]

[+]Means followed by the same letter are not significantly different at the 0.05 level according to Duncan's new multiple range test.

Table 26. Means of the yield of the landraces of sorghum. Well-watered and drought-stressed treatments have been averaged together.

Genotype	Yield
	g/plant
Segaolone	7.4[+b]
PI 494534	7.5[b]
PI 494544	10.6[ab]
PI 494551	12.8[a]

[+]Means followed by the same letter are not significantly different at the 0.05 level according to Duncan's new multiple range test.

SUMMARY AND CONCLUSION

Six physiological traits were measured on 16 genotypes of sorghum [Sorghum bicolor (L.) Moench] grown under well-watered or drought-stressed conditions in a commercial soil in a greenhouse to determine if wild sorghums and landraces can be used as sources of drought resistance. The six physiological traits measured were leaf water potential, leaf temperature, stomatal resistance, stomatal conductance, transpiration, and injury to cell membranes. The 16 genotypes represented five groups of sorghum: six wild sorghums; four landraces; two adapted, non-elite sorghums; two adapted, elite, drought-sensitive sorghums; and two adapted, elite, drought-resistant sorghums.

Differences due to genotype were not evident for transpiration and injury to cell membranes. Genotypic differences were significant for leaf water potential, leaf temperature, stomatal resistance, and stomatal conductance. Genotype x water interaction was not significant for these four traits.

Differences in leaf water potential were observed within the wild sorghums and the landraces and among the groups. Within the wild sorghums, IS14329 from South Africa had the lowest potential and 12-26 from Egypt had the

highest potential. Within the landraces, SN 537 (PI 494544) had the lowest potential and Segaolane from Botswana had the highest potential. The drought-resistant, elite sorghums did not have a higher or lower potential than that of the drought-sensitive, elite sorghums. Leaf water potential of drought-stressed plants was similar to that of well-watered plants except on two dates, when drought-stressed plants had a lower potential than well-watered plants.

Differences in leaf temperature were observed within the wild sorghums and among the groups. 12-26 from Egypt had the coolest leaf temperature. Mean leaf temperatures of the five groups of sorghum ranged from 28.1°C for the non-elite and drought-sensitive, elite sorghums to 29.0°C for the wild sorghums.

Differences in stomatal resistance were observed within the wild sorghums, within the landraces, and among the groups. Within the wild sorghums, IS14250 from Angola had the lowest stomatal resistance, and within the landraces, SN 537 (PI 494544) had the lowest stomatal resistance. The wild sorghums tended to have the lowest stomatal resistance among the groups. Differences in stomatal conductance were observed within the wild sorghums and among the groups. Within the wild sorghums, IS14250 from Angola had the

highest stomatal conductance. The wild sorghums had the highest stomatal conductance among the groups.

Significant water treatment differences were found for dry weight, but not for yield or height, which indicated that yield and height were not altered by drought. Differences in dry weight were observed within the wild sorghums, the landraces, the non-elite sorghums, and among the groups. Within the wild sorghums, 12-26 from Egypt had the lowest dry weight. Within the landraces, Segaolane from Botswana had the lowest dry weight. The non-elite sorghum, SC 35-6, had a higher dry weight than did the other non-elite sorghum, SC 118. Among the groups, the landraces had a higher dry weight than the other groups.

Differences in yield were observed within the landraces, the drought-resistant, elite sorghums, and among the groups. SN 543 (PI 494551) had the highest yield within the landraces. IA 28 (drought-resistant) yielded more than KS 65 (drought-resistant). Among the groups, the wild and non-elite sorghums had the lowest yield and the landraces and elite sorghums had the highest yield. The drought-resistant, elite sorghums had the largest yield among the sorghum groups.

Since genotype x water interaction was not significant for the physiological traits studied, it was difficult to

determine if wild sorghums and landraces could be used as sources of drought resistance for breeding programs. In this study, the drought-stressed plants were watered every 11 to 14 days and extremely severe water stress did not develop. More research should be done under very severe droughts to see if wild sorghums and landraces might be used as sources of drought resistance.

LITERATURE CITED

Ackerson, R.C., D.R. Krieg, and F.J.M. Sung. 1980. Leaf conductance and osmoregulation of field grown sorghum. Crop Sci. 20:10-14.

Blum, A. 1972. Effect of planting date on water-use and its efficiency in dryland grain sorghum. Agron. J. 64:775-778.

Blum, A. 1974. Genotypic responses in sorghum to drought stress. I. Response to soil moisture stress. Crop Sci. 14:361-364.

Blum, A. 1979. Genetic improvement of drought resistance in crop plants: a case for sorghum, p. 429-446. In H. Mussell and R. C. Staples (ed.) Stress physiology in crop plants. John Wiley and Sons, New York.

Blum, A. 1980. Genetic improvement of drought adaptation. p. 450-452. In N.C. Turner and P.J. Kramer (ed.) Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Blum, A. 1982. Evidence for genetic variability in drought resistance and its implications for plant breeding, p. 53-68. In Drought resistance in crops with emphasis on rice. Int. Rice Res. Inst., Los Banos, Laguna, Philippines.

Blum, A. 1983. Breeding programs for improving crop resistance to water stress. p. 263-275. In C.D. Raper, Jr., and P.J. Kramer (ed.) Crop reactions to water and temperature stresses in humid, temperate climates. Westview Press, Boulder, Colorado.

Blum, A. 1985. Breeding crop varieties for stress environments. CRC Critical Rev. Plant Sci. 2:199-238.

Blum, A. 1987. Review of book: The origins and domestication of cultivated plants. Ed by G. Barigozzi. Elsevier Sci. Pub., Amsterdam, The Netherlands. 1986. Field Crops Res. 16:363-365.

Blum, A. and G.F. Arkin. 1984. Sorghum root growth and water-use as affected by water supply and growth duration. Field Crops Res. 9:131-142.

Blum, A. and A. Ebercon. 1981. Cell membrane stability as a measure of drought and heat tolerance in wheat. Crop Sci. 21:43-47.

Blum, A. and C.Y. Sullivan. 1986. The comparative drought resistance of landraces of sorghum and millet from dry and humid regions. Ann. Bot. 57:835-846.

Blum, A., K.F. Schertz, R.W. Toler, R.I. Welch, D.T. Rosenow, J.W. Johnson, and L.E. Clark. 1978. Selection for drought avoidance in sorghum using aerial infrared photography. Agron. J. 70:472-477.

Brun, L.J., E.T. Kanemasu, and W.L. Powers. 1972. Evapotranspiration from soybean and sorghum fields. Agron. J. 64:145-148.

Brun, L.J., E.T. Kanemasu, and W.L. Powers. 1973. Estimating transpiration resistance. Agron. J. 65:326-329.

Chaudhuri, U.N. and E.T. Kanemasu. 1982. Effect of water gradient on sorghum growth, water relations and yield. Can. J. Plant Sci. 62:599-607.

Chaudhuri, U.N. and E.T. Kanemasu. 1985. Growth and water use of sorghum (Sorghum bicolor (L.) Moench) and pearl millet (Pennisetum americanum (L.) Leeke). Field Crops Res. 10:113-124.

Chaudhuri, U.N., M.L. Deaton, E.T. Kanemasu, G.W. Wall, V. Marcarian, and A.K. Dobrenz. 1986. A procedure to select drought-tolerant sorghum and millet genotypes using canopy temperature and vapor pressure deficit. Agron. J. 78:490-494.

Christiansen, M.N. 1982. World environmental limitations to food and fiber culture. p. 1-11. In M.N. Christiansen and C.F. Lewis (ed.) Breeding plants for less favorable environments. John Wiley and Sons, New York.

Durley, R.C., T. Kannangara, N. Seetharama, and G.M. Simpson. 1983. Drought resistance of Sorghum bicolor. 5. Genotypic differences in the concentrations of free and conjugated abscisic, phaseic and indole-3-acetic acids in leaves of field-grown drought-stressed plants. Can. J. Plant Sci. 63:131-145.

Garrity, D.P., C.Y. Sullivan, and D.G. Watts. 1984. Changes in grain sorghum stomatal and photosynthetic response to moisture stress across growth stages. Crop Sci. 24:441-446.

Harlan, J. R. and J.M.J. de Wet. 1972. A simplified classification of cultivated sorghum. Crop Sci. 12:172-176.

Henzell, R.G., K.J. McCree, C.H.M. van Bavel, and K.F. Schertz. 1975. Method for screening sorghum genotypes for stomatal sensitivity to water deficits. Crop Sci. 15: 516-518.

Henzell, R.G., K.J. McCree, C.H.M. van Bavel, and K.F. Schertz. 1976. Sorghum genotype variation in stomatal sensitivity to leaf water deficit. Crop Sci. 16:660-662.

Hicks, S.K., R.J. Lascano, C.W. Wendt, and A.B. Onken. 1986. Use of a hydraulic press for estimation of leaf water potential in grain sorghum. Agron. J. 78:749-751.

Huda, A.K.S., M.V.K. Sivakumar, Y.V. Sri Rama, J.G. Sekaran, and S.M. Virmani. 1987. Observed and simulated repsonse of two sorghum cultivars to different water regimes. Field Crops Res. 16:323-335.

Jain, S.K. 1983. Domestication and breeding of new crop plants. p. 177-197. In D.R. Wood, K.M. Rawal, and M.N. Wood (ed.) Crop breeding. Am. Soc. Agron., Crop Sci. Soc. Am., Madison, Wisconsin.

Jika, N.I., C.A. St.-Pierre, and J.C. Denis. 1980. The adaptation of varieties of sorghum to different water regimes. Can. J. Plant Sci. 60:233-239. (In French, Eng. sum.)

Jones, M.J. 1987a. Plant population, rainfall and sorghum production in Botswana. I. Results of experiment station trials. Exp. Agr. 23:335-347.

Jones, M.J. 1987b. Plant population, rainfall and sorghum production in Botswana. II. Development of farmer recommendations. Exp. Agr. 23:349-356.

Kanemasu, E.T. 1977. Evapotranspiration from corn, sorghum, soybean, and winter wheat. Keeping Up With Research No. 32. Kansas State Univ., Manhattan, Kansas. 4 p.

Kanemasu, E.T., A.-J. Chen, W.L. Powers, and I.D. Teare. 1973. Stomatal resistance as an indicator of water stress. Trans. Kansas Acad. Sci. 76:159-166.

Kanemasu, E.T., L.R. Stone, and W.L. Powers. 1976. Evapotranspiration model tested for soybean and sorghum. Agron. J. 68:569-572.

Kirkham, M.B., M.S. Redelfs, L.R. Stone, and E.T. Kanemasu. 1985. Comparison of water status and evapotranspiration of six row crops. Field Crops Res. 10:257-268.

Krieg, D.R. 1983. Sorghum p. 351-388. In I.D. Teare and M.M. Peet (ed.) Crop-water relations. John Wiley and Sons, New York.

Krieg, D.R., and R.B. Hutmacher. 1982. The utility of various drought resistance mechanisms. Proc. Annu. Corn Sorghum Ind. Res. Conf. 37:37-51.

Krieg, D.R., and R.B. Hutmacher. 1986. Photosynthetic rate control in sorghum: stomatal and nonstomatal factors. Crop Sci. 26:112-117.

Liang, G.H., A.D. Dayton, C.C. Chu, and A.J. Casady. 1975. Heritability of stomatal density and distribution on leaves of grain sorghum. Crop Sci. 15:567-570.

Majerus, W.J. 1987. Comparison of screening techniques for drought tolerance in grain sorghum. M.S. Thesis. Kansas State Univ., Manhattan, Kansas. 62 p.

Martin, J.H. 1971. Sorghum. Encycl. Brit. 20:920.

Myers, R.J.K., M.A. Foale, and A. Done. 1984. Responses of grain sorghum to varying irrigation frequency in the Ord irrigation area. III. Water relations. Aust. J. Agr. Res. 35:43-52.

Owonubi, J.J., and E.T. Kanemasu. 1982. Water use efficiency of three height isolines of sorghum. Can. J. Plant Sci. 62:35-46.

Peacock, J.M., S.N. Azam-Ali, and R.B. Matthews. 1985. An approach to screening for resistance to water and heat stress in sorghum [Sorghum bicolor (L.) Moench]. Paper presented at an International Arid Lands Research and Development Conference "Arid Lands: Today and Tommorrow", 20-25 Oct. 1985, Tucson, Arizona, U.S.A. Int. Crops. Res. Inst. Semi-Arid Tropics (ICRISAT), Patancherau, India. 25 p.

Quizenberry, J.E. 1982. Breeding for drought resistance and plant water use efficiency. p. 193-212. In M.N. Christiansen and C.F. Lewis (ed.) Breeding plants for less favorable environments. John Wiley and Sons, New York.

Ravindranath, P. and A. Shiv Raj. 1983. Effect of moisture stress on growth, yield and yield components of field-grown sorghum varieties having glossy and non-glossy leaves. Indian J. Agr. Sci. 53:428-430.

Rees, D.J. 1986a. The effects of population density and intercropping with cowpea on the water use and growth of sorghum in semi-arid conditions in Botswana. Agr. Forest Meteorol. 37:293-308.

Rees, D.J. 1986b. Crop growth, development and yield in semi-arid conditions in Botswana. II. The effects of intercropping Sorghum bicolor with Vigna unguiculata. Exp. Agr. 22:169-177.

Richardson, S.G., and K.J. McCree. 1985. Carbon balance and water relations of sorghum exposed to salt and water stress. Plant physiol. 79:1015-1020.

Stone, L.R., E.T. Kanemasu, and M.L. Horton. 1975. Grain sorghum canopy temperature as influenced by clouds. Remote Sensing Environ. 4:177-181.

Stout, D.G., and G.M. Simpson. 1978. Drought resistance of Sorghum bicolor. I. Avoidance mechanisms related to leaf water status. Can. J. Plant Sci. 58:213-224.

Sullivan, C.Y. 1972. Mechanisms of heat and drought resistance in grain sorghum and methods of measurement. p. 247-264. In N.G.P. Rao and L.R. House (ed.) Sorghum in seventies. Oxford and IBH Pub. Co., New Delhi.

Sullivan, C.Y. and W.M. Ross. 1979. Selecting for drought and heat resistance in grain sorghum. p. 263-281. In H. Mussell and R.C. Staples (ed.) Stress physiology in crop plants. John Wiley and Sons, New York.

Sumayao, C.R., E.T. Kanemasu, and T. Hodges. 1977. Soil moisture effects on transpiration and net carbon dioxide exchange of sorghum. Agr. Meteorol. 18:401-408.

Sumayao, C.R., E.T. Kanemasu, and T.W. Brakke. 1980. Using leaf temperature to assess evapotranspiration and advection. Agr. Meteorol. 22:153-166.

Szeicz, G., C.H.M. van Bavel, and S. Takami. 1973. Stomatal factor in the water use and dry matter production by sorghum. Agr. Meteorol. 12:361-389.

Teare, I.D. and E.T. Kanemasu. 1972. Stomatal-diffusion resistance and water potential of soybean and sorghum leaves. New Phytol. 71:805-810.

Teare, I.D., R. Manam, and E.T. Kanemasu. 1974. Diurnal and seasonal trends in nitrate reductase activity in field grown sorghum plants. Agron. J. 66:733-736.

van Bavel, C.H.M. and W.L. Ehrler. 1968. Water loss from a sorghum field and stomatal control. Agron. J. 60:84-86.

van Bavel, C.H.M., R.J. Lascano, and L. Stroosnijder. 1984. Test and analysis of a model of water use by sorghum. Soil Sci. 137:443-456.

Wright, G.C., R.C.G. Smith, and J.M. Morgan. 1983. Differences between two grian sorghum genotypes in adaptation to drought stress. III. Physiological responses. Aust. J. Agr. Res. 34:637-651.

EVALUATION OF DIFFERENT SORGHUM
GENOTYPES FOR DROUGHT RESISTANCE

By

PHODISO L. GAOSEGELWE

B.S., Kansas State University, 1985

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of
the requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

Kansas State University
Manhattan, Kansas

1988

ABSTRACT

Six physiological traits were measured on 16 genotypes of sorghum [Sorghum bicolor (L.) Moench] grown under well-watered or drought-stressed conditions in a commercial soil in a greenhouse to determine if wild sorghums and landraces can be used as sources of drought resistance. The six physiological traits measured were leaf water potential, leaf temperature, stomatal resistance, stomatal conductance, transpiration, and injury to cell membranes. The 16 genotypes represented five groups of sorghum: six wild sorghums; four landraces; two adapted, non-elite sorghums; two adapted, elite, drought-sensitive sorghums; and two adapted, elite, drought-resistant sorghums.

Differences due to genotype were not evident for transpiration or injury to cell membranes. Genotypic differences were significant for leaf water potential, leaf temperature, stomatal resistance, and stomatal conductance. Genotype x water interaction was not significant for these four traits. Differences in leaf water potential and stomatal resistance were observed within the wild sorghums and the landraces and among the groups. Differences in leaf temperature and stomatal conductance were observed within the wild sorghums and among the groups. No one group or genotype had a consistently high or low leaf water

potential, leaf temperature, stomatal resistance, or stomatal conductance throughout the study.

Significant water treatment differences were found for dry weight, but not for yield or height, which indicated that yield and height were not altered by drought. Differences in dry weight were observed within the wild sorghums, the landraces, the non-elite sorghums, and among the groups. Differences in yield were observed within the landraces, the drought-sensitive, elite sorghums, and drought-resistant, elite sorghums, and among the groups. The wild and non-elite sorghums had the lowest yield and the landraces and elite sorghums had the highest yield. The drought-resistant, elite sorghums had the largest yield among the sorghum groups.

Since genotype x water interaction was not significant for the physiological traits studied, it was difficult to determine if wild sorghums and landraces could be used as sources of drought resistance for breeding programs. In this study, extremely severe water stress did not develop. More research should be done under very severe droughts to see if wild sorghums and landraces might be used as sources of drought resistance.